Relationships between lamb carcass quality traits measured by X-ray computed tomography (CT) and current UK-hill sheep breeding goals.

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Relationships between lamb carcass quality traits measured by X-ray computed tomography and current UK hill sheep breeding goals

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Genetic parameters were estimated between current UK hill sheep breeding goals and lamb carcass composition and muscularity traits derived using X-ray computed tomography (CT). To produce these estimates, a total of 648 lambs from two hill farms were CT scanned at weaning (ca 120 days of age), over 3 years, and total weights of carcass muscle (MUSC), fat (CFAT) and bone (BONE) and internal fat (IFAT) were predicted. Previously derived muscularity indices were also calculated for the hind leg (HLMI) and lumbar (LRMI) regions, to assess muscle shape. Data for current breeding goals (lamb performance and maternal traits) were also included from a total of 10 297 lamb records and 12 704 ewe records. Heritabilities were estimated for each trait and genetic and phenotypic correlations were calculated between each CT trait and other lamb or ewe traits. Moderate to high positive genetic correlations were found between CT-predicted tissue weights and breeding goals, which were also weights (lamb weaning weight, carcass weight, mature ewe weight, average weight of lambs reared by the ewe). CFAT was positively genetically correlated with ultrasound backfat depth at weaning (UFD) and subjective fatness grade at slaughter (MLCF), suggesting that carcass fat could be decreased using selection on any of these predictors. Ultrasound muscle depth at weaning (UMD) and subjective conformation score at slaughter (MLCC) had high genetic correlations with the muscularity indices (HLMI and LRMI), but correlations with MUSC were not significantly different from zero. This implies that selection to improve MLCC is likely to be increasing the 'roundness' of muscle shape in the high-priced carcass region, but having little impact on total lean meat yield. Correlations of CT traits with the other ewe traits (number of lambs weaned, number of lambs lost, longevity, fleece weight) were generally small or not significantly different from zero. The genetic parameters generated in this study can now be used in selection index calculations to assess the benefits of including lamb CT traits in future selection programmes for hill sheep.

Keywords: body composition, carcass composition, computed tomography, genetic parameters, sheep

Introduction

Selection of an experimental line of hill sheep using a multi-trait index that includes both maternal and lamb performance traits has resulted in economic improvements when compared with a control line, on two experimental hill farms of contrasting environmental severity (Conington *et al*., 2006a). This research has been used as the basis for recommendations to the UK hill sheep sector and commercial hill sheep breeding programmes have adopted this index for selection of breeding stock (www.bfelite.co.uk, www.scottishsheepstrategy.org.uk). Much of the economic progress observed is due to improvements in maternal traits, such as number of lambs weaned and lamb survival, alongside increased weights of lambs at marketing (Conington *et al*., 2004). However, improvements in carcass quality traits have not been evident as a result of 7 years of selection on this index in the two experimental flocks. Minimal changes have been observed between the selection and control lines in traits such as subjective fatness and conformation scores awarded at the abattoir (Conington *et al*., 2006a), weights of fat, muscle and bone, or muscularity traits as measured using X-ray computed tomography (CT) scanning (Lambe *et al*., 2007). At present, the breeding goal traits in the index include subjective fatness and conformation scores, which are predicted from

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ultrasound fat and muscle depths on live lambs at weaning. These previous studies have suggested that including CT-derived traits in place of subjective carcass grades as breeding goals would preferentially accelerate improvement of carcass traits.

Heritabilities have been estimated for several CT-derived traits in hill lambs scanned at weaning, including predicted weights of fat, muscle and bone in the carcass, internal fat, and muscle shape traits (Conington *et al*., 2006b). However, before these traits can be included in the selection index for hill sheep, genetic and phenotypic relationships with the traits included in the current index must be estimated. The aim of this study was therefore to estimate genetic parameters for the current ewe and lamb traits in the index (using more animals and family groups that those originally used by Conington *et al*., 2001), and to examine the relationships among these and CT traits. This information can then be used to facilitate investigation into the relative merits of including CT-derived composition and muscularity traits in future selection programmes for hill sheep.

Material and methods

Farms and sheep flocks

Scottish Blackface sheep flocks from two SAC research hill farms of contrasting severity, that have been described in detail previously (Conington *et al*., 2001 and 2006a), were involved in the study. Both flocks were comprised of approximately 600 ewes. Performance and pedigree data have been collected at farm 1 since 1991 and at farm 2 since 1996.

Within each flock, three genetic lines were run together: the selection (S), control (C) and industry (I) lines. In the S line, animals retained for breeding were selected according to the highest score in a multi-trait selection index developed by Conington *et al*. (2001, 2004 and 2006a). Animals were selected for breeding in the C line with average index scores, and in the I line using normal commercial (visual) means. Selection within these genetic lines began in 1998 with the first lambs born into the lines in 1999. In addition, on both farms, 40 ewes per year were mated by artificial insemination to rams from the UK Blackface sire reference scheme – Blackface Elite – to provide genetic links with other commercial flocks (lambs referred to as line R).

CT scanning

A sample of lambs from each farm were CT scanned in 2003, 2004 and 2005 at weaning, giving a total of 648 lambs scanned. The distribution of lambs, according to farm, genetic line and year are presented in Table 1. A total of 495 lambs from farm 1 and 153 from farm 2 were CT scanned. Lambs were chosen at random from within sire within each line.

Age of lambs at scanning ranged from 96 to 145 days, with an average of 123 days. All lambs were born to ewes ranging from 2 to 6 years old (2 to 5 years old only at farm 2) and were reared either as singles (50%) or twins (50%). Within-farm, selected lambs from each line had the same

Table 1 *Count of lambs scanned within each farm, genetic line and year and total number of sires represented within each line on each farm*

	Farm 1				Farm 2			
LINE	2003	2004	2005	Total no. of sires	2003	2004	2005	Total no. of sires
S	61	63	50	11	24	19	20	5
C	80	66	54	13	25	20	18	6
I	18	16	54	6				0
$R^{\dagger}$	8	10	15	4	8	10	9	3
Total	167	155	173	34	57	49	47	14

$^{\dagger}R$ = lambs born to matings with reference sires from Blackface Elite.

average age (126 days at farm 1, 116 days at farm 2) and live weight (31 kg at farm 1, 26 kg at farm 2) at CT scanning, with similar standard deviations in each of these variates in each line.

The CT scanning procedures for these lambs, comprising cross-sectional reference scans and spiral scans, were described in full by Lambe *et al*. (2007). Previously derived prediction equations were used to estimate total weights of carcass fat, muscle, bone, and internal fat from cross-sectional images (Lambe *et al*., 2006). Image analysis on spiral CT scans allowed calculations of muscle volume in the hind leg and the lumbar region, as described by Navajas *et al*. (2006), and linear dimensions of the femur bone and spine, which were combined to produce values for muscularity indices in the hind leg (HLMI) and lumbar region (LRMI) for each lamb, following the method of Navajas *et al*. (2007). Increased values for these muscularity indices represented a greater volume of muscle relative to the length of the bone that it surrounds (De Boer *et al*., 1974; Purchas *et al*., 1991).

Data set

A summary of the traits studied, and the data available for each of these traits, is shown in Table 2. This included CT data from the 648 lambs, combined with further production data from 10 297 lambs from farm 1 and 5393 lambs from farm 2. Ewe production records were also included from farm 1 (7332 records) and farm 2 (5372 records).

For one lamb with very low fat levels, carcass fat (CFAT) was predicted as negative, using the established prediction equation, and for another lamb internal fat (IFAT) was predicted as negative. Since a negative tissue weight is not biologically possible, these two values were set to zero. However, it is unlikely that these lambs had no carcass fat or internal fat, but that they had very minimal amounts that could not be clearly detected in the CT images.

All available lambs were ultrasonically scanned at weaning. Male lambs were slaughtered at a commercial abattoir when they reached commercial slaughter criteria in terms of minimum live weights (usually $\sim$37.5 kg live weight, depending on abattoir specifications in a given year or season) and condition scores (target score of 3, on a subjective scale of 0 to 5; Jefferies, 1961).

Table 2 *Summary of traits included in the data set*

	Trait	Description	Count	Mean	s.d.	Min.	Max.
CT traits	CFAT	Predicted carcass fat weight (kg)	648	1.83	0.89	0	4.77
	MUSC	Predicted muscle weight (kg)	648	7.12	1.04	3.80	10.14
	BONE	Predicted bone weight (kg)	648	2.29	0.28	1.45	3.15
	IFAT	Predicted internal fat (kg)	648	0.81	0.28	0	1.77
	HLMI	Hind leg muscularity index	648	5.92	0.37	4.11	7.18
	LRMI	Loin muscularity index	648	0.72	0.07	0.50	0.99
Lamb traits	WWT	Weaning live weight (kg)	15515	28.4	4.7	10.4	49.5
	UFD	Ultrasound fat depth (cm)	14970	0.19	0.11	0.01	0.97
	UMD	Ultrasound muscle depth (cm)	14972	2.00	0.25	0.83	2.91
	DCWT	Carcass weight (kg)	5682	17.1	2.6	9.5	29.3
	MLCF	MLC fat grade[†]	6272	11.0	1.7	4	20
	MLCC	MLC conformation grade[†]	6324	2.74	0.68	1	5
Ewe traits	PMWT	Pre-mating live weight (kg)	12 407	53.6	7.1	31.0	83.0
	LWEAN	No. of lambs reared to weaning[‡]	13 352	1.11	0.71	0	3
	LLOST	No. of lambs lost by weaning[§]	11 008	0.21	0.46	0	3
	TOTWWT	Litter weight[¶] (kg)	10 309	38.8	13.2	10.4	104.6
	LONGV	Age at culling/death (years)	3645	4.50	1.00	1	6
	FLWT	Fleece weight (kg)	4709	1.99	0.47	0.19	3.71

CT = X-ray computed tomography.
[†]Converted to numerical scales as described by Conington *et al.* (2001).
[‡]Including ewe's own lambs only.
[§]Including lambs still born/fostered off/taken off for other reasons.
[¶]Including lambs fostered on. Divided by number of lambs at weaning to give maternal weaning weight (MATWWT).

Data analysis

Heritabilities for each CT, lamb or ewe trait were estimated using univariate analyses in ASREML (Gilmour *et al.*, 2001). Random models fitted in ASREML included a direct genetic effect (animal) and an ewe effect. In the case of the lamb traits (including CT traits), the effect of ewe represented a maternal permanent environmental effect (c^2), whereas for the ewe traits this represented a permanent environmental effect (*pe*) between parities. The inclusion of a maternal genetic effect was only significant for three of the lamb traits (weaning weight (WWT), ultrasound backfat depth at weaning (UFD), ultrasound muscle depth at weaning (UMD)), and the effect was very small, resulting in non-significant differences in the heritabilities estimated. These small and inconsistent results may be due to the limited volume or structure of the data for some of the traits. As a result, and to remain consistent across traits, a maternal genetic effect was not fitted for any trait.

The following fixed effects models were fitted for each trait:

$$\begin{aligned}\text{lamb trait} = {} & \text{age} + \text{farm} + \text{year} + \text{sex} + \text{rear rank 1week} \\ & + \text{damage} + \text{grazing} + \text{farm} \times \text{year} \\ & + \text{farm} \times \text{sex},\end{aligned}$$

$$\begin{aligned}\text{ewe trait} = {} & \text{age} + \text{farm} + \text{year} + \text{grazing} \\ & + \text{farm} \times \text{year} + \text{farm} \\ & \times \text{age} \ (+\text{weaning category} + \text{lamb breed}),\end{aligned}$$

where '$\times$' represents an interaction between terms.

For lamb traits, age was measured in days (covariate) and was the age at which the relevant measurement was taken, whereas for ewe traits age was measured in years (factor). The factor 'grazing' coded for the field or area that the animal was grazing at weaning (for lamb traits) or pre-mating (for ewe traits). Pre-mating grazing reflects the home-range area that is predominantly grazed by each animal. Rearing rank at 1 week was chosen over litter size or rearing rank at weaning for lamb traits, since this was thought likely to have the largest impact on early growth and development. To allow correlations with the *average* weight of lambs reared to weaning (MATWWT), the variate *total* litter weight weaned by the ewe (TOTWWT) was adjusted for 'weaning category' (a factor with six levels combining the number and sex of lambs reared to weaning). 'Lamb breed' was also fitted in the MATWWT model describing the breed of lambs reared to weaning – pure Scottish Blackface (in 96.4% of records), lambs from a Scottish Blackface ewe crossed to a Texel (in 124 records $\approx$ 1.2%), or Cheviot (in 106 records $\approx$ 1%) sire, or a white-faced cross-bred lamb (in 141 records $\approx$ 1.4%) of unknown breed.

The covariate age was significant for each trait. Each fixed effect and/or interaction was significant for the majority of traits, although not every fixed effect was significant for each trait. However, to remain consistent, the same models were fitted across groups of traits. The only exceptions were for fleece weight (FLWT) (grazing and farm $\times$ age omitted, since this trait was only recorded once per ewe and all measurements were taken at 1 year old on farm 1) and longevity (LONGV) (grazing, age, farm $\times$ age and ewe effect omitted, since only measured once in an ewe's lifetime).

Genetic line was not included as a fixed effect in the models, as it was not significant for the majority of traits (CT, lamb or ewe traits) when fitted in the model. For the few traits where it was significant, it did not significantly affect the genetic variance or heritability estimated. This suggests that the cumulated selection differential was insufficient (mainly due to the low number of generations of selection) to produce significant line divergence in most components of the multi-trait index. Since the purpose of these estimates of genetic parameters was their possible inclusion in selection index calculations, and nearly all analyses contained one of the traits upon which selection was performed, genetic line was not included in any of the models.

The pedigree file included records from 18 453 animals. This included a maximum of nine generations of pedigree data for the lambs included in the data set. The majority of lambs with CT records had pedigree information on all four grandparents (527 of the 648 lambs) and at least four great-grandparents (559 lambs), with 325 lambs having pedigree information from all eight great-grandparents.

Correlations (genetic and phenotypic) between CT traits and other lamb or ewe traits were estimated using bivariate analyses in ASREML. Multivariate analyses were attempted, but would not converge. For bivariate analyses between two lamb traits, covariance between ewe (maternal permanent environmental) effects for each trait was also fitted in the random model. This covariance was significant and reduced the log likelihood value in the majority of pairwise analyses, suggesting an improved model. The exceptions were the bivariates of UMD with IFAT, HLMI and LRMI, and MLC fat grade (MLCF) with LRMI, where the analyses would not converge when a covariance between ewe effects was included, so this term was omitted.

Results

Genetic parameters

Heritabilities for lamb traits (including CT traits) were moderate in size with the exception of IFAT, which had a low heritability (Table 3). Maternal permanent environmental effects were small to moderate for most lamb traits, but close to zero for muscularity indices and MLC carcass grades.

Pre-mating (mature) ewe weight (PMWT) and FLWT had moderate heritabilities, MATWWT was less heritable, and number of lambs weaned (LWEAN), number of lambs lost (LLOST) and LONGV had very low heritabilities. The only ewe trait with a significant permanent environmental effect was PMWT.

Relationships between CT traits and lamb or ewe traits

Genetic correlations between lamb CT traits and lamb or ewe traits are shown in Table 4 and phenotypic correlations in Table 5. Large standard errors (s.e.) were estimated for many of the genetic correlations, in particular those including traits with low heritabilities (IFAT, LWEAN, LLOST, LONGV) or traits that were difficult to standardise in their measurement (carcass weight (DCWT), MLCF, MLC conformation grade (MLCC)). These carcass traits were partly constrained by abattoir specifications, and MLCF and MLCC were scored subjectively. The genetic correlations with LLOST, LONGV and IFAT have not been presented in Table 4 as they were too imprecise to be meaningful.

Table 3 *Univariate heritabilities (h^2), ewe effects (c^2 or pe) and phenotypic variances (σ_p^2) for each trait (with s.e. in parenthesis)*

	Trait	h^2	c^2 or *pe*	σ_p^2
CT traits	CFAT	0.25 (0.11)	0.25 (0.08)	0.48 (0.03)
	MUSC	0.35 (0.12)	0.28 (0.08)	0.66 (0.03)
	BONE	0.36 (0.13)	0.16 (0.08)	0.04 (0.002)
	IFAT	0.07 (0.07)	0.15 (0.08)	0.06 (0.003)
	HLMI	0.47 (0.13)	0.09 (0.08)	0.10 (0.01)
	LRMI	0.17 (0.09)	0.08 (0.08)	0.003 (0.0002)
Lamb index traits	WWT	0.24 (0.02)	0.16 (0.01)	14.22 (0.20)
	UFD	0.22 (0.02)	0.10 (0.01)	0.01 (0.0001)
	UMD	0.33 (0.02)	0.08 (0.01)	0.05 (0.001)
	DCWT	0.25 (0.11)	0.26 (0.08)	2.38 (0.13)
	MLCF	0.21 (0.03)	0.01 (0.02)	2.20 (0.04)
	MLCC	0.19 (0.03)	0.01 (0.07)	0.33 (0.01)
Ewe index traits	PMWT	0.38 (0.03)	0.25 (0.02)	27.87 (0.54)
	LWEAN	0.06 (0.01)	0.04 (0.01)	0.46 (0.01)
	LLOST	0.03 (0.01)	0.03 (0.01)	0.21 (0.003)
	MATWWT	0.16 (0.02)	0.03 (0.02)	26.99 (0.41)
	LONGV	0.03 (0.02)	–	0.78 (0.02)
	FLWT	0.52 (0.03)	–	0.17 (0.004)

CT = X-ray computed tomography.

Very high genetic and phenotypic correlations with WWT were estimated for MUSC and BONE. Moderate to high phenotypic correlations with WWT were also estimated for CFAT and IFAT, although the genetic correlation with CFAT was lower. Phenotypic correlations of WWT with muscularity indices (HLMI and LRMI) were also moderate and positive, although genetic correlations were not significant.

Phenotypic correlations with DCWT were moderate and positive for CFAT, MUSC and BONE, and small and positive for IFAT, HLMI and LRMI. Genetic correlations of DCWT with the tissue weight traits were all moderate and positive, but with the muscularity indices were small. However, large s.e. limit the reliability of the genetic correlations with this trait.

Moderate to high phenotypic correlations were estimated between ultrasound measurements at weaning (UFD, UMD) and all CT traits. UFD was most highly correlated with CFAT and then with IFAT, whereas UMD was most highly correlated with MUSC, HLMI and LRMI. Positive genetic correlations with UFD were also estimated for CFAT and muscularity indices (higher genetic correlation with LRMI). UMD had strong, positive genetic correlations with HLMI and LRMI, but the genetic correlation with MUSC was not significant.

MLCF was only significantly positively correlated, both at the genetic and phenotypic levels, with CFAT. Phenotypic

Table 4 *Genetic correlations between lamb CT traits and current index or goal traits (s.e. are shown in parenthesis)*

	Trait	CFAT	MUSC	BONE	HLMI	LRMI
Lamb traits	WWT	0.30 (0.16)	0.85 (0.06)	0.95 (0.04)	0.21 (0.15)	0.03 (0.21)
	UFD	0.62 (0.17)	−0.16 (0.18)	−0.15 (0.18)	0.27 (0.15)	0.44 (0.19)
	UMD	−0.05 (0.21)	0.13 (0.15)	−0.04 (0.16)	0.63 (0.09)	0.93 (0.07)
	DCWT	0.42 (0.28)	0.37 (0.23)	0.49 (0.25)	0.03 (0.23)	−0.28 (0.36)
	MLCF	0.67 (0.28)	−0.24 (0.25)	−0.16 (0.25)	−0.12 (0.23)	0.16 (0.30)
	MLCC	−0.003 (0.31)	0.12 (0.28)	−0.19 (0.26)	0.71 (0.22)	0.91 (0.27)
Ewe traits	PMWT	0.68 (0.16)	0.89 (0.11)	0.90 (0.12)	0.30 (0.15)	0.40 (0.22)
	LWEAN	−0.18 (0.30)	−0.01 (0.26)	0.13 (0.26)	−0.004 (0.23)	−0.31 (0.38)
	MATWWT	0.97 (0.10)	0.98 (0.07)	0.97 (0.09)	0.60 (0.12)	0.62 (0.17)
	FLWT	0.001 (0.15)	0.16 (0.13)	0.05 (0.13)	−0.06 (0.11)	−0.04 (0.17)

CT = X-ray computed tomography.

Table 5 *Phenotypic correlations between lamb CT traits and current index or goal traits (s.e. are shown in parenthesis)*

	Trait	CFAT	MUSC	BONE	IFAT	HLMI	LRMI
Lamb traits	WWT	0.70 (0.02)	0.87 (0.01)	0.83 (0.01)	0.40 (0.03)	0.49 (0.03)	0.33 (0.04)
	UFD	0.70 (0.02)	0.36 (0.04)	0.27 (0.04)	0.43 (0.03)	0.36 (0.04)	0.31 (0.04)
	UMD	0.44 (0.03)	0.55 (0.03)	0.39 (0.04)	0.25 (0.04)	0.57 (0.03)	0.52 (0.03)
	DCWT	0.30 (0.07)	0.30 (0.06)	0.34 (0.06)	0.10 (0.08)	0.13 (0.07)	0.13 (0.08)
	MLCF	0.28 (0.07)	−0.02 (0.08)	0.04 (0.08)	0.08 (0.09)	0.06 (0.08)	−0.01 (0.09)
	MLCC	0.13 (0.08)	0.07 (0.08)	0.09 (0.08)	0.05 (0.09)	0.22 (0.07)	0.14 (0.08)
Ewe traits	PMWT	0.24 (0.06)	0.39 (0.05)	0.39 (0.05)	0.08 (0.06)	0.13 (0.06)	0.11 (0.06)
	LWEAN	−0.02 (0.04)	−0.002 (0.04)	−0.02 (0.04)	−0.05 (0.03)	−0.001 (0.04)	−0.03 (0.03)
	LLOST	0.01 (0.04)	0.08 (0.03)	0.09 (0.03)	−0.06 (0.03)	0.01 (0.04)	0.03 (0.03)
	MATWWT	0.30 (0.04)	0.39 (0.04)	0.34 (0.04)	0.11 (0.04)	0.20 (0.04)	0.14 (0.04)
	LONGV	0.05 (0.06)	0.06 (0.06)	0.02 (0.06)	−0.05 (0.07)	0.05 (0.07)	−0.01 (0.06)
	FLWT	0.0004 (0.07)	0.09 (0.07)	0.03 (0.07)	0.02 (0.06)	−0.04 (0.07)	−0.02 (0.07)

CT = X-ray computed tomography.

relationships between MLCC and CT traits were weak, whereas genetic correlations with HLMI and LRMI were strong and positive. Correlations between MLCC and MUSC were not significant.

Moderate phenotypic correlations were estimated between carcass tissue weights measured by CT in lambs (CFAT, MUSC, BONE) and PMWT or MATWWT of ewes. At the genetic level, these correlations were very high. Positive genetic correlations were also estimated between these ewe traits and HLMI or LRMI.

Correlations (phenotypic or genetic) between CT traits and LWEAN tended to be negative, but were not significantly different form zero. Phenotypic correlations between LLOST and CT traits were close to zero. Genetic correlations between these traits had very large s.e. and are not presented. Similarly, genetic correlations with LONGV could not be interpreted reliably due to large s.e. Relationships between CT traits and FLWT were not significantly different from zero.

Discussion

The multi-trait selection index for hill sheep currently in use in the UK includes the breeding goal traits of MLCC, with a positive weighting, and MLCF, with a negative weighting, as well as UFD and UMD as predictor traits that can be measured on all live lambs. However, improvements in carcass quality, in terms of fat and conformation scores, have been predicted to be minimal, albeit with a predicted increase in carcass weight (Conington *et al.*, 2001). The use of CT-derived traits in the index, either in the breeding goals in place of these subjective scores, or as measured traits, may help to accelerate improvements in carcass composition. The genetic parameters and relationships described here for all relevant traits will allow this hypothesis to be tested.

The CT traits measured on Scottish Blackface lambs at weaning were moderately heritable (with the exception of IFAT), suggesting that genetic selection on these traits would be successful. Heritabilities for the current index and goal traits are in general agreement (differences of <0.1 for all traits) with those estimated from the same Scottish Blackface flocks several years ago, as part of a previous study, which provided the data on which the index was based (Conington *et al.*, 2001). Heritabilities of CFAT and MUSC in the present study were similar to those for UFD and UMD. The heritability estimate for UMD is similar in magnitude to those estimated for terminal sire breeds in the UK (Jones *et al.*, 2004) and for various breeds

in New Zealand (Nsoso *et al*., 2004). However, in terminal sire studies (Jones *et al*., 2004; Kvame and Vangen, 2007), as well as another study involving Scottish Blackface lambs (Karamichou *et al*., 2006), heritabilities of MUSC derived by CT were slightly higher (0.45 to 0.48) than the 0.35 found here. The heritability for UFD was at the lower end of the range found in other studies in different breeds and crosses (Wolf and Smith, 1982). Estimates of heritabilities for CFAT in terminal sire breeds in the UK and Norway (Jones *et al*., 2004; Kvame and Vangen, 2007) ranged from 0.18 to 0.41. A much higher heritability of 0.6 was estimated for CFAT in Scottish Blackface lambs by Karamichou *et al*. (2006). Heritabilities estimated here were close to those found in cross-bred lambs for MLCF (Wolf *et al*., 1981; Jones *et al*., 1999), and for MLCC in the study by Wolf *et al*., although the estimate from Jones *et al*. was slightly higher ($\sim$ 0.24). This low heritability suggests that genetic progress in MLCC is likely to be slow, particularly as part of a multi-trait selection index involving several other (possibly conflicting) traits. Higher heritabilities were estimated here for most of the CT traits, compared with MLCF or MLCC.

The genetic correlations suggest that including selection for increased MUSC in a breeding programme for Scottish Blackface sheep would be associated with increased lamb weights at weaning (WWT, MATWWT) and slaughter (DCWT). However, unfavourable increases may occur in mature ewe weights and numbers of lambs lost. Results from Coopworth sheep in New Zealand, selected for 14 years on weight-adjusted ultrasound measurements, found that ewes from a line selected for increased leanness were significantly heavier pre-mating and had lower lamb survival than controls or those from a line selected for high fat depth (McEwan *et al*., 2001). CT studies on Scottish Blackface ewes have shown that MUSC in breeding ewes at different times throughout the annual reproductive cycle is positively genetically correlated with number of lambs born and total weight of litter reared (Lambe *et al*., 2005). The current results suggest that MUSC in the lamb is also associated with increased weights of lambs reared (MATWWT), but not number of lambs weaned (LWEAN). McEwan *et al*. (2001) found no difference between their fat, lean or control Coopworth lines in number of lambs weaned per ewe mated, but lean line ewes had higher weights of lamb weaned per ewe.

The genetic correlations also imply that increased CFAT in lambs may be associated with higher MATWWT, but decreased LWEAN in ewes. Genetic correlations with the important weight traits (WWT, DCWT, MATWWT) were similar or higher with MUSC and BONE than with CFAT, suggesting that reducing CFAT, but increasing MUSC would not have a large negative effect on these traits, which also agrees with the results from the Coopworth study. CFAT and IFAT in breeding Scottish Blackface ewes at mating and before lambing have also been found to be positively genetically correlated with average weight gain of lambs during rearing (Lambe *et al*., 2005). Preliminary genetic correlations estimated between CT-derived predicted tissue weights in lambs and in breeding ewes suggest that they are under similar genetic control (N. Lambe, unpublished results).

It is important to note that live weight was included in the prediction equations, alongside CT tissue areas and densities, to estimate CFAT, MUSC and BONE, in order to achieve the most accurate predictions. In CT studies of lambs from terminal sire breeds (Macfarlane, 2006), it was found that including live weight in the prediction equations for tissue weights increased the genetic correlations amongst the tissue weights and between tissue weights and live weights. This could lead to problems with co-linearity in multi-trait genetic evaluations of tissue weights alongside live weights, and may inflate estimates of covariances, making index scores less reliable (Macfarlane, 2006). In the results presented here and by Conington *et al*. (2006b) for Scottish Blackface lambs, the genetic correlations between CFAT and WWT or MUSC were only moderate in size. However, the genetic correlation between WWT and MUSC was very high. It may therefore be preferable to use MUSC in place of WWT, rather than including both in a multi-trait index. This should be considered in any future selection index development.

Although positive genetic correlations were anticipated between CT carcass tissue weights (CFAT, MUSC, BONE) and other body weight traits (WWT, DCWT, PMWT, MATWWT), the correlations estimated with MATWWT are extremely high, and higher even than those with direct WWT measured on the lamb, of which these CT traits are constituents. The phenotypic correlations are lower, and closer to the magnitude expected. The genetic correlation between WWT and MATWWT was also very high (0.997). Therefore, although the precise values of these genetic correlation estimates may be unfeasibly high, live weights from weaning to adulthood appear to be under very similar genetic control.

Jones *et al*. (2004) and Kvame and Vangen (2007) found genetic correlations between UMD and MUSC ranging from 0.42 to 0.7 in terminal sire lambs. The estimate here is substantially lower (0.13) and UMD seems to be more highly correlated to muscularity indices than MUSC in this breed. A high genetic correlation (0.56) between UMD and MLCC was also estimated (although correlations between existing index traits are not presented here), suggesting that UMD is a good predictor of conformation and muscularity in Scottish Blackface lambs, but not necessarily of total lean yield. These results suggest that if carcasses continue to be graded using the current MLC conformation scores, then selection using UMD should result in improvements in this trait. However, since selection for carcass quality traits in hill breeds must be done within the context of a multi-trait selection index including maternal traits, modest changes in carcass traits have been predicted with the current index (Conington *et al*., 2001). Stronger correlations with HLMI and in particular LRMI suggest that selection using CT-derived measured muscularity indices,

in place of UMD or as a second stage of selection, may be more effective at improving MLCC. The low genetic correlation of MUSC with MLCC agrees with results comparing MLCC with dissected lean weight in cross-bred lambs (Jones *et al*., 1999), although higher genetic correlations between MLCC and lean percentage have been estimated in other breeds (e.g. Wolf and Smith, 1982). This implies that selection for total muscle weight would not improve this subjective conformation trait in hill lambs, and conversely selection to improve MLCC is likely to be having little impact on total lean meat yield. A high genetic correlation, in line with those from previous dissection studies (Wolf and Smith, 1982; Jones *et al*., 1999), suggests that selecting for reduced CFAT would, however, be successful in reducing MLCF in hill lambs. CFAT was not significantly genetically associated with MLCC in the Scottish Blackface lambs studied, so simultaneous selection for increased conformation and decreased total carcass fat should be possible. In this breed, MLCC (a subjective, visual assessment of carcass shape, which in theory could be influenced by muscle and fat; Anderson, 2003) does not appear to be confounded with total carcass fat weight.

New grading systems are currently being tested in the UK that use video image scanning and analysis of carcasses in the abattoir to estimate total carcass lean yield, amongst other traits. If future payment schemes from these grading systems were to reward for such carcass characteristics, then the results from this study suggest that UMD may not be an accurate predictor of total muscle weight in the carcass of hill lambs. Alternative measurement techniques, such as CT scanning, may then become more relevant in sheep breeding schemes.

Muscularity in the hind leg (HLMI) appears to be either uncorrelated, or favourably genetically correlated with most of the current goal traits. Genetic relationships with muscularity in the loin (LRMI) are less clear, due to large s.e. associated with several correlations, but suggest that increased muscularity in this region may be associated with a reduction in LWEAN and an increase in LLOST. These relationships should be investigated further using a data set with an increased number of lamb CT records, before recommendations about the inclusion of LRMI in the hill sheep index can be made.

These parameters should now be used as the basis for selection index calculations to look at the effects of including CT-derived composition and muscularity traits in the hill sheep multi-trait selection index. Future work will report on the implications of using CT-derived carcass traits in the breeding goal, and alongside maternal traits that are an integral component of breeding programmes in the UK.

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